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Cover Page Footnote

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The Motion Aftereffect: A Review of Mechanisms and Variants

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ABSTRACT

The motion aftereffect causes a visual stimulus to undergo apparent motion. An adapting stimulus, which moves in a specific direction, adapts motion-responsive neurons in the middle temporal area (V5) to that direction of motion. Viewing a second stimulus, known as a test stimulus, produces apparent motion in the direction opposite that of the initial stimulus. Neural networks involved in attention and working memory are also implicated in the motion aftereffect. Despite extensive documentation in the literature, there is little known about the mechanisms of the motion aftereffect. This review discusses established knowledge of the motion aftereffect, focusing primarily on the middle temporal area. Variants of the motion aftereffect that are in line with the established mechanism are discussed, namely the phantom motion aftereffect and sensory-contingent motion aftereffects, which incorporate color and visual surroundings into the production of the motion aftereffect. This optical illusion provides insight into motion processing as well as memory.

The motion aftereffect causes a visual stimulus to undergo apparent motion. Looking at a moving "adapting stimulus" for a substantial period of time and then switching to another "test stimulus," which can be stationary or moving, will cause apparent motion in the direction opposite that of the initial stimulus. Discussed as early as the 4th century BCE by Aristotle, it is an illusion that can be easily observed with several types of moving stimuli. An aftereffect can be produced with translational, rotational, expanding, or contracting stimuli (Macpherson & Baysan, 2017). Despite its long history, the neural mechanisms of the motion aftereffect are still being studied, and fascinating variants of the conventional motion aftereffect are being discovered, many of which are a consequence of the neural mechanisms. In this review, the mechanisms of the motion aftereffect will be examined with a focus on the middle temporal area, and major motion aftereffect variants will be discussed.

MECHANISMS OF THE MOTION AFTEREFFECT

THE MIDDLE TEMPORAL AREA

The middle temporal area, also known as MT or V5, is one of the areas of the visual cortex that contributes to the motion aftereffect. This part of the visual cortex has large receptive fields and contains direction-specific, motion-responsive neurons. Neurons in the MT are particularly responsive to rotational motion, and they receive motion signals from the primary visual cortex (V1). Further processing of these signals leads to the motion aftereffect. However, other types of motion produce activity in the MT as well, including translational motion, expansion, and contraction (Mather, 2015, p. 483).

One of the initial studies that showed a motion aftereffect could be observed in the MT was conducted using functional magnetic resonance imaging (fMRI). The adapting stimuli were concentric rings that either expanded or contracted. After the adaptation period, a stationary image of the same type was shown. For a control, rings that alternated between expanding and contracting over the adaptation period were used. When accounting for the fMRI signal produced during the control condition, 70% of the excitation signal due to the motion aftereffect was found to come from the MT (Tootell et al., 1995, p. 139). While other areas of the visual cortex were excited due to this illusion, the MT was predominant. Given the direction-sensitivity of the MT and the consistent apparent motion of a test stimulus opposite to that of the adapting stimulus, the strong involvement of the MT in this illusion seems logical.

If the MT is involved in the motion aftereffect, changes in the brain that parallel changes in apparent motion should be observed. The above study was able to track these changes. The percentage change in fMRI signal was recorded during exposure to a single motion adapting stimulus, a test stimulus, a control stimulus, and then another test stimulus. Sharp increases in activity during exposure to both the adapting stimulus and the control were seen. However, the signal remained high for a substantial amount of time only after the single motion condition. This is defined as the fMRI motion aftereffect,

and it had a decay time of 8.3 seconds vs. 9.2 seconds for the psychophysical motion aftereffect, or the effect observed by test subjects. These times were labeled "essentially identical" by the authors (Tootell et al., 1995, pp. 139-140). The similar decay times are significant because they support the substantial involvement of the MT in the motion aftereffect. It is possible that the psychophysical effect lasts slightly longer because of a delayed perceptual response to changes in MT signaling, or simply because keeping track of qualitative changes such as this requires sharp focus from test subjects. Even if the delay is not due to these factors, motion aftereffect decay follows a similar pattern in perception as well as in the brain.

CONTRAST GAIN AND RESPONSE GAIN

The initially held belief regarding the mechanism of the motion aftereffect in the MT was that it functions via response gain, which describes the maximum firing rate of a cell. However, another likely mechanism is contrast gain, meaning the motion aftereffect is mediated by changes in the sensitivity of direction-sensitive neurons. A study conducted by Adam Kohn and J. Anthony Movshon (2003) explored the responses of MT neurons to sine wave gratings to determine the correct mechanism. Several populations of neurons were tested to gather data about multiple motion directions. Test stimuli with varying contrasts were shown both before and after adaptation to a grating that moved in the direction preferred by the cell being studied. Changes in response and contrast gain were measured. MT neurons were adapted to stimuli primarily by contrast gain. Because neuronal responses showed consistent shifts following adaptation to stimuli of different contrasts, they could be displayed with a mathematical equation. These shifts were clearly represented on a plot of response against contrast, suggesting that MT neurons were involved in the motion aftereffect. Also, the shift of the steep portion of the curve to higher contrasts indicates that the cells in the middle temporal area become less sensitive to contrasts that would have normally provoked a response. This suggests that following adaptation, a stronger stimulus in the cell's preferred direction is needed for firing.

ATTENTIONAL NETWORKS IN THE MOTION AFTEREFFECT

Though the MT has been declared by many as the major cortical area involved in the motion aftereffect, there are critics that say it does not account for the attentional demands of the motion aftereffect, which are best observed outside of the occipital cortex. In a brain activity study by Hautzel et al. (2001, p. 282), for instance, this was the only cortical area observed. In addition, it is believed that attention can enhance the motion aftereffect (Mather et al., 2008, p. 485). Using positron emission tomography (PET) and measurements of cerebral blood flow, multiple interconnected regions of the cortex were found to be activated due to attention. The activated regions were found alongside the activated MT and other areas of the visual cortex. These attention-mediating regions include the anterior cingulate cortex, the parietal cortex, and the right DLPFC (Hautzel et al., 2001, pp. 289-291). The fact that none of these areas is explicitly involved in visual processing supports the prediction that the motion aftereffect activates cortical areas that have other functions and are located outside of the visual cortex.

It is important to note, however, that the MT likely remains at the root of the motion aftereffect, along with other areas of the visual cortex such as V1. Because the motion aftereffect is a visual illusion, these areas are essential for a motion aftereffect to be perceived, while the attentional networks appear to strengthen it. Nevertheless, their interconnectedness suggests they might all be activated in response to the motion aftereffect. Notably, the study by Hautzel et al. (2001) does not mention exactly how these areas communicate. Therefore, more research is needed in this area.

A VARIANT PRODUCED BY LARGE RECEPTIVE FIELDS IN THE MT: PHANTOM MOTION AFTEREFFECT

Because the cells in the MT have large receptive fields, a variant known as the phantom motion aftereffect can sometimes be observed. This occurs when a region of a test stimulus outside of the retinal area that was adapted appears to move. One of the first studies that suggested the existence of the phantom motion aftereffect was conducted by Robert J. Snowden and Alan B. Milne (1997). Adapting stimuli consisted of moving dots in two opposing quarters of a circle. Tests for the traditional, or concrete, motion aftereffect used those same moving dots, except the coherence level was varied to make the adaptation and test stimuli move the same way. The phantom test was performed similarly, but the two unadapted quarters of the circle were filled with dots instead. A significantly higher coherence in the adapting motion direction was needed in both test stimuli for them to appear identical to the adapting stimulus, compared to the baseline in which subjects were not adapted. However, the phantom aftereffect was weaker than the concrete aftereffect (pp. 718-719). The significant difference between the baseline and phantom conditions indicates that a phantom motion aftereffect does exist. The nullification of the phantom stimuli also shows this, since nullification implies that cells in the MT are using contrast gain to change how a stimulus is perceived.

The phantom motion aftereffect was also seen using stationary test stimuli, known as a static motion

aftereffect, and the importance of global adaptation in the motion aftereffect was shown in a study by Alan Lee and Honjing Lu (2014). Like in the study by Snowden and Milne, the phantom condition was nullified at a coherence level significantly higher than the control condition, but the phantom condition was not significantly different than the concrete condition, which adapted both local and global processing (Lee and Lu, 2014, pp. 773-775). The phantom motion aftereffect functions at the global level of visual perception. The motion aftereffect generally requires that an adapting stimulus have a global, or overall, direction of motion (Snowden & Milne, 1997, p. 717). Without this, a motion aftereffect could not be perceived since the resulting apparent motion is opposite to the adapting motion. The lack of a significant difference between the concrete and phantom conditions supports the idea that the motion aftereffect originates primarily from global motion.

AWARENESS OF THE ADAPTING DIRECTION: IS IT NECESSARY?

As stated previously, a global motion direction is necessary for the phantom motion aftereffect to occur, and this applies for most concrete forms of the motion aftereffect. However, this is not true in cases where the adapting stimulus has multiple adapting directions. This situation prevents subjects from consciously perceiving a global adaptation direction, but adaptation at the local level can still occur. Additionally, this motion aftereffect variant will occur on a global scale when viewing the test stimulus.

To show that multiple adapting directions make the global adapting direction imperceptible, Gabor elements arranged in a circle were grouped into 1-5 sets, and each set had a different global translational motion direction. In addition, another type of Gabor stimulus, in which each element moved in a random direction, was presented to determine if subjects could correctly guess which pattern contained random movement. A similar procedure was used with four Gabor stimuli that underwent clear clockwise, expanding, and contracting motion to establish a benchmark, since these should have been easily identified as non-random. A "mixed" condition was also presented using complex motion, in which four groups of different motion patterns were used. The mixed condition and the patterns with 3-5 sets of translational motion directions were considered indistinguishable from a completely random stimulus, based on the accuracy of selecting the random stimulus, which was at or below chance level for these conditions (Lee & Lu, 2014, pp. 766-769). This finding shows that the ability to perceive complex stimuli as non-random disappears with more groups in an adapting pattern.

STATIC MOTION AFTEREFFECT

Based on the finding by Lee and Lu (2014), subjects were tested to see if they could perceive a static motion aftereffect from a complex Gabor stimulus, which had 5 equally sized sets of elements that moved in five different translational directions. There were two conditions for the test stimuli, which were stationary. The first condition used Gabor elements from one set, therefore they had been moving in a single direction during adaptation. The second condition stimulus used ⅕ of the elements from each set, and this functioned as a control. Though the adapting stimulus was multidirectional and had no clear global adaptation direction, the test stimulus with elements from one set still yielded a motion aftereffect, as determined by a dial that participants turned in the direction of apparent motion. There was a clear consensus that the direction of apparent motion was 180° from the direction of adapting motion, while in the mixed condition no direction prevailed (Lee & Lu, 2014, pp. 770-771). A 180° angle is formed by two lines completely opposite each other, so in this case it indicates that the direction of apparent motion is completely opposite the adapting motion direction. This suggests that subjects were unconsciously processing all five directions of motion in the adapting stimulus. Since only one set of elements appeared in the test stimulus, only one of the processed directions was used to produce a motion aftereffect.

DYNAMIC MOTION AFTEREFFECT AND PROCESSING AT THE LOCAL

Another study carried out by Lee and Lu (2014) provided a relative measure of the strengths of various motion aftereffects, using a protocol similar to Snowden and Milne (1997) in their paper on the phantom motion aftereffect. Specifically, the motion coherence levels in the test stimuli were varied to gauge the strength of the motion aftereffect produced in each condition. Adaptation at the local and global levels was observed using four different conditions. One of the conditions, the local condition, was analogous to the single motion condition in the static motion aftereffect study. Because those subjects adapted to motion in multiple directions and were tested on stimuli moving in only one of those directions, they experienced a motion aftereffect at the local level. The other conditions included a test for global adaptation using a phantom motion aftereffect, a condition in which both local and global processing levels were adapted, and a "neither" condition in which no adaptation was expected to occur. The three adaptation conditions were all significantly different from the control based on the coherence level needed to nullify the motion aftereffect, indicating that a motion aftereffect was perceived at local and global levels (Lee & Lu, 2014, pp. 773-775).

The idea that a motion aftereffect can be perceived when only the local level of motion processing is adapted appears to be a departure from established knowledge, but this is not so. Early studies of the motion aftereffect tended to use adapting stimuli that moved in a single, clearly identifiable direction, and test stimuli were either stationary or also moved in a single direction. Because of this, it is understandable that the local level of motion processing would be overlooked. In addition, Lee & Lu (2014) showed that though local motion aftereffects were possible, the strongest motion aftereffects are given via adaptation at the global level, and when both levels are adapted there is no significant difference in strength compared to when only the global level was adapted (p. 775). This indicates that most of the motion aftereffect comes from global adaptation, which concurs with previous studies. Local adaptation plays a smaller role and because of the complexity of stimuli that isolate local adaptation, it is unlikely that effects of this nature would be common outside of a lab environment.

SENSORY-CONTINGENT MOTION AFTEREFFECTS

As discussed from the perspective of multidirectional stimuli and the use of varying coherence levels to nullify a motion aftereffect, there are various ways that stimuli can be modified to create variants of the motion aftereffect or change its strength. Additionally, sensory features such as color can augment the motion aftereffect (Favreau et al., 1972). The presence of additional shapes or figures in the visual field can change the way a motion aftereffect is perceived as well (Nakashima et al., 2015). Motion aftereffect variants such as these are known as sensory-contingent motion aftereffects because they rely on a sensory property besides motion to produce an aftereffect. Taken together, these phenomena fit in well with the knowledge that the motion aftereffect relies on higher-level visual processing through cortical areas such as the MT, which contains cells with wide receptive fields.

SURROUNDINGS-CONTINGENT MOTION AFTEREFFECTS

When an adapting stimulus is presented inside a frame of a certain shape, the presence of that same frame in the test stimulus can produce a surroundings-contingent motion aftereffect. This means that the shape of the frame is associated with the direction of motion in the adapting stimulus. Just as the standard motion aftereffect causes apparent movement in the opposite direction of the movement in the adapting stimulus, the surroundings-contingent motion aftereffect causes apparent movement opposite of the direction in which the adapting stimulus moved when presented with a shaped frame, provided that frame is presented again with the test stimulus (Nakashima et al., 2015, pp. 9-10).

This was shown by Nakashima et al. (2015) using rightward and leftward moving dots surrounded by square or circle frames. Half of test subjects were shown rightward moving dots in a circular frame and leftward moving dots in a square frame, and the other half of test subjects were shown leftward moving dots surrounded by a circular frame and vice versa. The right and left-moving stimuli were alternated over 90 seconds. Then, a test stimulus with low motion coherence (ranging from -30 to 30%, where positive numbers indicate the adapting direction) was shown with the circular frame, the square frame, and alone. Participants experienced a left-moving test stimulus when it was presented with the frame that had surrounded the right-moving dots. The opposite was also reported. In addition, this effect was observed when the adapting stimuli were present at either the same retinal or the same spatial locations, as well as when both locations were the same. However, when both locations differed, a surroundings-contingent motion aftereffect was only observed if the two stimuli were in the same hemifield (pp. 10-12). Hemifields are halves of the visual field in each eye, and each hemifield corresponds to a different half of the visual cortex. Thus, Nakashima et al. (2015) supported the ability of the motion aftereffect to "spread" outside of the adapting region in the retina and in space, but only to a certain extent. Overall, the results suggest that, besides gathering information about global motion, the visual cortex can use information about the entire scene to create a motion aftereffect.

COLOR-CONTINGENT MOTION AFTEREFFECTS

The color of an adapting stimulus can also be associated with a particular aftereffect. Similar to the surroundings-contingent motion aftereffect, presenting a test stimulus with a color that was associated with a particular direction in the adapting stimulus can produce apparent motion opposite to the direction the stimulus moved in the adapting phase. Unlike the Nakashima et al. (2015) study, Favreau et al. (1972) used a static test stimulus to show this as opposed to a dynamic one. The adapting stimulus was a black line formed into a three-turn spiral, known as an Archimedean spiral. It was placed on a screen and rotated clockwise to give the appearance of contraction, and counterclockwise to give the appearance of expansion. This movement alternated after a set time interval to allow observers to adapt to both directions. The contracting spiral was illuminated by green light for half of the observers and red light for the other half, the expanding spiral was illuminated by red and green light respectively for the two groups. When exposed to stationary, green-illuminated spirals following adaptation, those who had been shown green contracting

spirals during adaptation saw the stationary green spirals expanding, and vice versa. The same effect was seen with red-illuminated test spirals.

This color-contingent motion aftereffect suggests that, in addition to shapes, color can be associated with different motion aftereffects. As with other sensory-contingent motion aftereffects, two adapting stimuli must be shown to cause a direction to be associated with a particular sensory property. This brings up the question of how many stimuli with different properties can be shown during adaptation to give sensory-associated motion aftereffects. It is possible that adaptation to five directions with five corresponding colors or frame shapes, for example, may be too much for the visual system to handle. However, since unconscious adaptation with multidirectional stimuli has been observed (Lee & Lu, 2014), showing more than two adapting stimuli may be able to give more than two motion aftereffects.

CONCLUSIONS AND FUTURE STUDY

The motion aftereffect primarily originates from the direction-sensitive cells in the MT, where higher-level visual processing takes place (Mather, 2015, p. 483). As such, the motion aftereffect can occur on unadapted areas of the receptive field, and properties besides motion can be associated with a motion aftereffect. This brings up the possibility of new, undiscovered variants of the motion aftereffect. These variants may also provide insight into the mechanisms of adaptation to visual stimuli.

Further study is needed on multiple aspects of the motion aftereffect. First, communication between the visual cortex and cortical areas responsible for attention and memory must be explored, as it is unclear how these areas work together (Hautzel et al., 2001). Sensory-contingent motion aftereffects need attention as well, in order to determine how many different sensory properties can be used to produce a unique motion aftereffect during a single adaptation session. Finally, it has been established that being tested on information in the same location it was learned in aids recall. Since the motion aftereffect utilizes cortical areas associated with working memory (Hautzel et al., 2001), and sensory motion aftereffects can last 24 hours after adaptation (Nakashima et al., 2015, p. 9), it would be interesting to see if location can be associated with a particular motion aftereffect following various time intervals.

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